

NON-VASCULAR EPIPHYTE DIVERSITY PATTERNS IN THE CANOPY OF AN UPPER MONTANE RAIN FOREST (2550–3670 m), CENTRAL CORDILLERA, COLOMBIA

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ABSTRACT. The presence and abundance of species in communities at a given moment may be looked at in two ways: (1) emphasizing the quality or quantity of the preceding propagule supply or (2) within community interactions, such as competition. Several studies have attributed great importance to the former in the organization of epiphyte communities based on observed distribution patterns of epiphytes and the high variability between epiphyte communities at apparently identical habitats. On the other hand, the great cover and biomass of bryophytic epiphyte vegetation in the tropical montane rain forest suggests that competitive interactions may also be of importance. In this study, the structural development of epiphyte communities (assumed to be positively correlated with branch diameter) in the canopy of a Colombian Upper Montane Rain Forest is analyzed. Sampling of the epiphyte vegetation included recording the presence and relative abundance of species and the total biomass of the community. Access to the canopy was obtained using rope-climbing techniques. Epiphyte sampling of 21 high standing trees revealed that canopy communities are rich in non-vascular epiphytes comprising 120 taxa of bryophytes and 61 taxa of macro lichens. Four community types are recognized that correspond to a certain position from outer towards inner canopy. The types share many species and therefore form an organizational unit. Species richness of each of these four abstract types is similar at about c. 100 taxa. However, concrete stands of epiphyte vegetation on the thick inner canopy branches (diam. 21–80 cm) comprised significantly less taxa ($p < 0.001$) per unit surface area than those on the thinner middle canopy branches ($5 \geq \text{diam.} \leq 20 \text{ cm}$), carrying on average 1.72 and 3.24 taxa/dm², respectively. Richness was significantly higher again in the outer canopy (diam. < 5 cm) with 7.81 taxa/dm². The opposite pattern would be expected when the time available for the immigration of species determines community richness. The decrease in variety with age is paralleled with an increase in biomass and a decrease in evenness. Thick branches and trunks typically carry large patches of individual plants of bryophytes, suggesting competitive replacement of species through 'horizontal' growth.

INTRODUCTION

A number of observations on epiphyte communities have led to the postulation that their actual composition and structure may depend largely on the quality and quantity of the preceding propagule supply. First, the variability between stands of epiphytes is often great and not easily attributed to differences in habitat (Schuster 1957, Barkman 1958, Johansson 1974, Yeaton & Gladstone 1982, Oksanen 1988, Ingram & Nadkarni 1993, Wolf 1993a,b). For example, in a related study, the complex environmental variables 'position within the host tree' and 'altitude' merely explain 3.2 % of the variance in the species data (Wolf 1994). Second, neighbouring trees regularly show greater epiphyte similarity than distant trees (Barkman 1958; Madison 1979; Catling *et al.* 1986). Third, the number of epiphytic species on isolated trees in pastures showed a negative correlation with the distance from the forest edge (Hietz-Seifert *et al.*

in press). Fourth, an altitudinal belt in the Colombian Andes of maximum liverwort richness coincided with a transition zone of overlapping distributions between the two distinct floras of lower and higher elevation (Wolf 1993c). Finally, many researchers believe that non-vascular epiphyte communities are far removed from a state of competitive equilibrium (Slack 1977, Watson 1980, During & Van Tooren 1988). This presumably facilitates the successful establishment of invading species. For vascular epiphytes, the occurrence of competition has not yet been demonstrated (Benzing 1990).

Island biogeography theory encompasses aspects of the arrival of species, and it also may provide the tools to explain species diversity patterns in the canopy, regarding individual branches as islands (MacArthur & Wilson 1967). Island biogeography theory predicts high species richness per unit of surface area on the thicker branches and tree trunks where the time available for the immigration of species presumably has been longer, assuming similar distances to the source, a great species pool and similar habitat heterogeneity at branches of different diameters.

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In contrast to the expected increase of species richness in time when aspects of the propagule supply are stressed, competitive interactions would lead to a decrease in richness due to a progressive exclusion of species. The occurrence of competition is suggested by the characteristic great biomass and cover of non-vascular epiphytes in the Upper Montane Rain Forest, *sensu* Grubb (Grubb 1974, Wolf 1993b, Miehe & Miehe 1994). Branch and trunk surfaces are typically shrouded by a 'sleeve' of bryophytes, even in the canopy.

Previous studies on diversity patterns in the canopy have mainly focussed on vascular epiphytes. The trend is that diversity and abundance are positively correlated with branch or trunk diameter (Johansson 1974, Wallace 1981, Yeaton & Gladstone 1982, Catling & Lefkovitch 1989, Ter Steege & Cornelissen 1989, Zimmerman & Olmsted 1992). However, when a correction is made for unit surface area, such differences may not be detected (Ingram & Nadkarni 1993). Invariably, the interpretation of the results is problematical. The patchiness of the vegetation raises the question of whether sampling was adequate, and the identification of sterile plants is often not possible. Moreover, it is unclear whether or not juvenile plants should be included, because they have a high mortality rate (Benzing 1981) and may never attain the reproductive stage. These difficulties are even more critical when distant observation methods are applied.

The study of non-vascular epiphytes offers several advantages over their vascular cohabitants. First, many young plants are already vigorous propagule suppliers by regularly producing spores in abundance and/or having extensive vegetative propagation (Richards 1984). Second, the classification of a sterile individual is often possible. Third, many species are widely distributed, allowing for a comparison at species level between distant areas. Fourth, species are often small relative to tree surface areas, allowing for many (>20) species to coexist on a few dm^2 . In this way, not only sampling is facilitated, but also the analysis of within-community processes. Finally, adequate sampling is more easily achieved. As to the latter, species/area curves for non-vascular epiphytes in the tropics indicate that sampling of 4–5 trees may yield much of the total flora (Gradstein *et al.* 1990, Wolf 1993c).

Knowledge about the distribution of non-vascular epiphytes in the tropical forest is incomplete and, with respect to the canopy, virtually lacking. The available data show that the canopy is rich in species, many of which are exclusive (Gradstein *et al.* 1990, Wolf 1993a,b, Sillett *et al.* in press). Within the canopy of a lowland rain

forest in Guyana, most species were present in the outer section, a pattern confirmed by the Colombian lower montane rain forest (Cornelissen & ter Steege 1989, Wolf 1993a). However, in the canopy of the Colombian forest at a higher elevation, no great differences in species richness within the canopy could be detected (Wolf 1993b).

In this study, non-vascular epiphyte diversity patterns, including both the variety and the relative abundance of species, in the canopy of a tropical upper montane rain forest are assessed in detail. Epiphyte diversity is examined in two ways: (1) the pattern shown by the (abstract) community types and (2) that of concrete stands on branch segments. Trends in succession in terms of the quality, richness and relative cover of species and their total biomass are suggested by comparing epiphyte assemblages on canopy branches of varying thickness. The strength of association between the variables is evaluated using the Spearman rank correlation coefficient, r_s .

METHODS

Fieldwork was carried out in undisturbed mountain forests on the west slope of the Central Cordillera, near the town of Santa Rosa de Cabal, Department of Risaralda, Colombia, at c. $4^{\circ}50'N$, $75^{\circ}30'W$, during intervals in 1985, 1986 and 1988. The forest is dominated by tree species of *Weinmannia* (Cunoniaceae), and may be classified as Upper Montane Rain Forest (Grubb 1974). Four host trees were selected at each of seven sites at 2550, 2740, 2970, 3110, 3370, 3510 and 3670 m elevation. Trees having an extremely coarse, smooth or sloughing bark were avoided, as were trees near the edge of the forest. Fast growing pioneer species were also excluded in the analysis, since these trees carried a different epiphyte community, leaving 21 host trees in nine species (Wolf 1993b, 1994).

The climate above 2500 m is cool and humid. Average daily temperature decreases with altitude from c. 12°C at 2500 m to c. 4°C near the treeline at 3670 m altitude (Witte 1994). Annual rainfall is 1250–2000 mm, without a pronounced dry season. Average daily relative humidity in clearings is above 80% and the air relative humidity in the canopy rarely drops below 70% (Wolf 1993a).

Access to the canopy was obtained using a slightly modified rope climbing technique (ter Steege & Cornelissen 1988, Wolf 1993a). The presence and abundance (in cover percentages) of epiphytes was estimated in plots positioned on the upper half cylinder of branch or trunk segments. All non-vascular plants were gathered, dried and their total living biomass was deter-

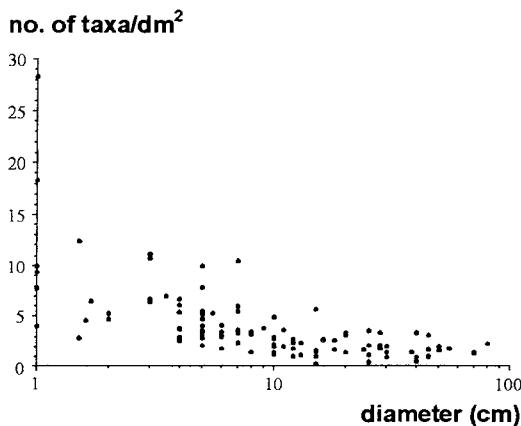


FIGURE 1. Branch or trunk diameter (cm) and non-vascular epiphyte species richness (S/dm^2).

mined to the nearest 0.1 gram. Plot size varied between one and over 20 dm^2 , 6.98 dm^2 on average.

Approximately 90% of the bryophytes and macro lichens encountered could be classified to species. The classification of crustose lichens, less abundant in the canopy, was more problematical. Therefore, crustose lichens are not considered in this study. More details on the methods, the study area and its climate are provided by Wolf (1993a,b).

RESULTS

The non-vascular epiphyte flora is rich in species, comprising 120 taxa of bryophytes and 61 macro lichens.

Based on criteria of the Zürich-Montpellier approach to vegetation analysis (Westhoff & Van der Maarel 1973), four community types are recognized (Wolf 1993b). These community types have many species in common and may be seen as a natural unit of integrating communities (TABLE 1). Moving inwards from the outer canopy, typically representative samples of the *Diplasiolajeunea pauckertii*-*Usnea* spp. community (A), the *Oropogon bicolor*-*O. loxensis* community (B), the canopy 'typicum' community (C) and the *Plagiochila fuscolutea* community (D) are subsequently encountered on a single branch.

As expected, lichen richness decreases towards the inner canopy, in contrast with bryophytes (TABLE 2). There are no great differences in total richness between epiphyte community types, even though variety in the middle tree crown is slightly higher, particularly in mosses. However, the richness per unit surface area of concrete stands of vegetation on individual branch segments var-

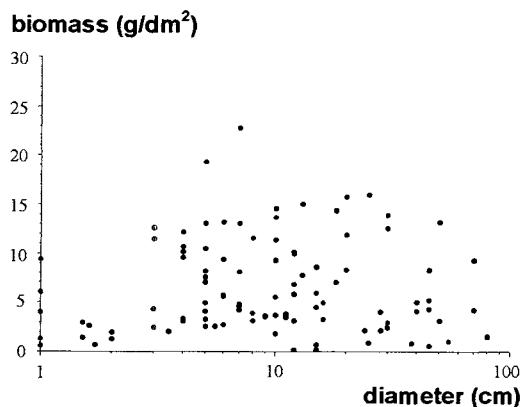


FIGURE 2. Branch or trunk diameter (cm) and biomass (g dryweight/ dm^2).

ies greatly (FIGURE 1). On individual branches, epiphyte richness generally decreases towards the inner canopy. Outer canopy twigs (diam. < 5 cm) support significantly ($p < 0.001$) more species (7.81 taxa/ dm^2) than middle canopy branches ($5 \geq$ diam. ≤ 20 cm; 3.24 taxa/ dm^2), which in turn host significantly more species than the thickest branches and trunks (diam. > 20 cm; 1.72 taxa/ dm^2).

The changes in species richness with branch diameter, coincide with structural changes. First, standing crop varies widely (FIGURE 2), having only a weakly positive correlation with branch diameter ($r_s = 0.02$; $p = 0.85$). The thinnest twigs, diam. c. 1 cm, carry a relatively large amount of epiphytic green biomass, due to an abundance of bryophytes and lichens that have a pendulous growth form, e.g. *Frullania peruviana* and *Usnea* spp. On branches of intermediate thickness, the biomass is either high or low. Diameters of over 30 cm pertain to erect tree trunks, accounting for the relatively low biomass values. Biomass is only weakly negatively correlated with species richness (FIGURE 3), but stronger so when only biomass values of over 3 g/dm^2 are considered ($r_s = -0.17$; $p = 0.11$). Communities that are rich in species generally have intermediate biomass values. Second, a significant decrease in evenness, expressed by the reciprocal Simpson index, occurs with increasing branch diameter, $r_s = -0.33$, $p < 0.001$ (FIGURE 4). In the 'climax' inner canopy communities, the most dominant species covers over 60 % of the substrate on average and the first three species in rank cover together over 90 %, leaving little space for other epiphytes, in particular bark epiphytes. A group of samples, indicated by open circles, do not concur well with the trend of increasing dominance with diameter. These communities also differ in

TABLE 1. Synoptic table of epiphyte communities in the canopy of the Upper Montane Rain Forest at Santa Rosa de Cabal. In addition to the presence degree (P) of species their cover in percentages is given (av. = average cover when present). Only the most common and/or characteristic non-vascular plants are included. For a full table see Wolf (1993b).

Community type Number of samples	A 25			B 32			C 47			D 47			
	P %	Cover %		P %	Cover %		P %	Cover %		P %	Cover %		
		-	av										
Common canopy taxa in the Upper Montane Rain Forest at Santa Rosa de Cabal.													
<i>Adelanthus decipiens</i> (Hook.) Mitt.		6	<1	<1	<1	19	<1	<1	1	2	<1	<1	<1
<i>Adelanthus pittieri</i> (Steph.) Grolle		34	<1	9	60	43	<1	15	99	34	<1	7	85
<i>Anastrophyllum auritum</i> (Lehm.) Steph.		25	<1	<1	2	13	<1	<1	1	6	<1	<1	<1
<i>Anoplolejeunea conferta</i> (Meissn.) Steph.	64	<1	1	5	56	<1	<1	5	45	<1	1	15	11
<i>Anzia leucobates</i> (Nyl.) Müll. Arg.	16	<1	1	3	13	<1	<1	<1	4	<1	<1	<1	<1
<i>Bazzania brevetiana</i> (Lindenb. & Gott.) Trevis.		13	<1	2	5	15	<1	1	2	4	<1	<1	<1
<i>Bazzania hookeri</i> (Lindenb.) Trevis.		9	<1	<1	1	66	<1	13	60	66	<1	12	90
<i>Bazzania longistipula</i> (Lindenb.) Trevis.	12	<1	<1	1	13	<1	9	30	17	<1	2	2	<1
<i>Campylopus pittieri</i> Williams/C. <i>fragilis</i> (Brid.) B.S.G.		13	<1	<1	<1	43	<1	4	60	45	<1	6	65
<i>Cheilolejeunea</i> spp.	24	<1	2	5	19	<1	1	1	15	<1	<1	6	<1
<i>Chorisodontium mittenii</i> (C. Müll.) Broth.	4	<1	<1	<1	63	<1	4	30	55	<1	8	60	87
<i>Cladonia</i> cf. <i>ochrochlora</i> Flk.		13	<1	<1	<1	23	<1	<1	1	6	<1	<1	1
<i>Daltonia longifolia</i> Tayl.	12	<1	<1	1	3	1	1	1	6	<1	1	2	<1
<i>Dictyonema glabratum</i> (Spreng.) D. Hawksw.	8	<1	<1	1	16	<1	5	20	17	<1	1	6	5
<i>Drepanolejeunea</i> spp.	64	<1	<1	1	56	<1	<1	1	43	<1	<1	2	9
<i>Everniastrum cirrhatum</i> (Fr.) Hale		12	1	2	2	9	<1	<1	2	5	5	5	5
<i>Frullania convoluta</i> Lindenb. & Hampe	28	1	3	5	44	<1	3	10	17	<1	5	15	2
<i>Harpalejeunea ancistroides</i> (Spruce) Schiffn.	12	<1	<1	1	28	<1	<1	<1	4	<1	<1	<1	<1
<i>Herbertus juniperoides</i> (Sw.) Grolle		9	<1	<1	<1	19	<1	11	55	9	<1	10	35
<i>Herbertus pensilis</i> (Tayl.) Spruce		34	<1	2	5	38	<1	22	60	26	<1	10	85
<i>Herbertus subdentatus</i> (Steph.) Fulf.	4	<1	<1	<1	41	<1	7	62	9	<1	5	15	32
<i>Heterodermia vulgaris</i> (Vain.) Follm. & Redon	12	<1	<1	<1	3	<1	<1	<1	6	<1	<1	<1	<1
<i>Hypotrachyna bogotensis</i> (Vain.) Hale	36	<1	6	45	38	<1	6	30	15	<1	3	20	4
<i>Hypotrachyna caraccensis</i> (Tayl.) Hale	16	<1	6	15	34	<1	8	30	4	2	4	5	4
<i>Hypotrachyna gigas</i> (Kurok.) Hale		22	<1	3	10	6	<1	2	5	15	<1	<1	1
<i>Hypotrachyna imbricatula</i> (Zahlbr.) Hale	8	2	2	2	28	<1	4	15	19	<1	2	10	
<i>Hypotrachyna laevigata</i> (Smith) Hale—group	60	<1	4	10	59	<1	4	32	34	<1	4	40	4
<i>Hypotrachyna microblasta</i> (Vain.) Hale	12	<1	4	10	16	<1	2	3	6	<1	<1	2	
<i>Hypotrachyna physcoides</i> (Nyl.) Hale	36	<1	4	25	69	<1	13	70	15	<1	9	40	6
<i>Hypotrachyna prolongata</i> (Kurok.) Hale	4	1	1	1	6	1	6	10	6	<1	2	5	2
<i>Hypotrachyna reducens</i> (Nyl.) Hale	24	1	4	6	9	<1	2	5	2	5	5	5	
<i>Jamesoniella rubricaulis</i> (Nees) Grolle s. lat.	4	<1	<1	<1	44	<1	11	40	60	<1	16	65	13
<i>Lepicolea pruinosa</i> (Tayl.) Spruce		63	<1	2	13	74	<1	7	30	91	<1	13	98

TABLE 1. Continued.

Community type Number of samples	A 25			B 32			C 47			D 47						
	P %	Cover %		P %	Cover %		P %	Cover %		P %	Cover %					
		-	av													
<i>Lepidozia</i> spp.	8	<1	<1	<1	56	<1	2	10	66	<1	3	25	43	<1	9	80
<i>Leptoscyphus jackii</i> (Steph.) Grolle	4	1	1	1	47	<1	13	70	15	<1	5	20	23	<1	10	35
<i>Leptoscyphus porphyrius</i> (Nees) Grolle	24	<1	<1	1	69	<1	2	15	96	<1	4	30	21	<1	1	1
<i>Menegazzia</i> sp. A (# 993)	20	1	2	5	16	<1	2	5	2	<1	<1	<1	<1	<1	<1	<1
<i>Metgeria decipiens</i> (Mass.) Schiffn.	12	<1	<1	1	13	<1	<1	2	11	<1	<1	<1	6	<1	1	2
<i>Normandina pulchella</i> (Borr.) Nyl.	28	<1	<1	<1	19	<1	<1	<1	6	<1	<1	<1	2	<1	<1	<1
<i>Plagiochila corniculata</i> Dum.	8	<1	<1	<1	6	<1	<1	<1	11	<1	<1	<1	6	<1	<1	1
<i>Plagiochila echinella</i> Gott. group	32	<1	3	10	91	1	19	55	89	<1	18	75	21	<1	12	55
<i>Prionodon fusco-lutescens</i> Hampe	4	5	5	5	19	<1	5	20	4	<1	3	5	13	<1	2	5
<i>Riccardia</i> spp.	40	<1	1	5	47	<1	2	10	28	<1	1	5	13	<1	<1	<1
<i>Sphaerophorus formosanus</i> (Zahlbr.) Asah.	4	1	1	1	25	<1	3	10	19	<1	<1	2	28	<1	<1	2
<i>Squamidium leucotrichum</i> (Tayl.) Broth.	8	<1	<1	<1	13	<1	<1	2	21	<1	<1	4				
<i>Sticta</i> cf. <i>damaeornis</i> (Sw.) Ach.					13	1	5	10	4	10	15	20	19	<1	6	10
<i>Sticta</i> spp.	8	<1	<1	<1	25	<1	18	60	30	<1	4	15	6	1	14	35
<i>Trachylejeunea dominicensis</i> Steph.	12	<1	<1	<1	34	<1	<1	2	9	<1	<1	2	<1	<1	<1	<1
<i>Trichocolea tomentosa</i> (Sw.) Gott.	4	<1	<1	<1	9	<1	1	2	17	<1	<1	2	30	<1	1	6
<i>Zygodon squarrosus</i> (Tayl.) C. Müll.					9	<1	<1	<1	2	1	1	13	<1	29	82	
Canopy taxa with a preference for the two outer canopy communities, types A and B.																
<i>Oropogon bicolor</i> Essl.	84	<1	4	10	81	<1	2	6	51	<1	<1	5	17	<1	<1	<1
<i>Oropogon loxensis</i> (Fée) Th. Fr.	76	<1	2	5	56	<1	1	5	19	<1	<1	6	<1	<1	<1	<1
<i>Microlejeunea</i> spp.	88	<1	<1	2	56	<1	<1	5	28	<1	<1	2	11	<1	<1	<1
<i>Aureolejeunea paramicola</i> (Herz.) Schust.	72	<1	5	15	47	<1	3	6	21	<1	2	10	13	<1	<1	1
<i>Leptoscyphus cuneifolius</i> (Hook.) Mitt.	64	<1	1	5	50	<1	<1	2	13	<1	<1	6	<1	<1	<1	<1
<i>Everniastrum catabiense</i> (Degel.) Hale	64	<1	3	8	41	<1	<1	5	4	<1	<1	2	<1	<1	<1	<1
<i>Frullania peruviana</i> Gott.	60	<1	4	25	56	<1	4	20	13	<1	1	2	23	<1	1	5
<i>Drepanolejeunea andina</i> Herzog	40	<1	1	2	28	<1	2	10	6	<1	<1	9	<1	<1	<1	<1
Canopy taxa with a preference for the <i>Diplasiolejeunea pauckertii</i> - <i>Usnea</i> spp. community, type A.																
<i>Diplasiolejeunea pauckertii</i> (Nees) Steph.	100	<1	1	3	25	<1	<1	<1	15	<1	<1	4	<1	<1	<1	<1
<i>Usnea</i> spp.	100	2	20	40	91	<1	3	10	55	<1	<1	5	23	<1	<1	1
Crustose lichen indet	80	<1	5	15	28	<1	5	10	6	<1	8	15	2	1	1	1
Graphidaceae	64	<1	9	30	19	1	8	30	2	1	1	1				
<i>Ramalina</i> sp. A (# 793)	52	<1	<1	5	9	<1	<1	<1	9	<1	<1	2	<1	<1	<1	<1
<i>Frullania</i> cf. <i>paradoxa</i> Lehm & Lindenb.	40	<1	5	20	6	<1	<1	<1								
<i>Colura naumannii</i> (Schiffn.) Steph.	28	<1	<1	<1	3	<1	<1	<1								
<i>Frullania tetraptera</i> Nees & Mont.	28	<1	<1	1	3	<1	<1	<1	4	<1	<1	<1				

TABLE 1. Continued.

Community type Number of samples	A			B			C			D		
	P %	— av	+	P %	— av	+	P %	— av	+	P %	— av	+
<i>Hypotrichyna sinuosa</i> (Smith) Hale	28	<1	<1	2								
<i>Megalospora tuberculosa</i> (Fee) Sipm.	24	10	3	10								
<i>Colura tenuicornis</i> Steph.	20	<1	<1	<1								
Canopy taxa with a preference for the canopy "typicum" community, type C.												
<i>Frullania brasiliensis</i> Raddi												
<i>Anastrophyllum piligerum</i> (Nees) Steph.												
Canopy taxa with a preference for the <i>Plagiochila fuscolutea</i> community, type D.												
<i>Plagiochila fuscolutea</i> Tayl.	6	1	3	5	32	<1	2	10	55			
<i>Porotrichodendron superbum</i> (Tayl.) Broth.	3	<1	<1	<1	15	<1	10	55				
<i>Lophocolea quadrivalvata</i> Spruce												

other aspects and are apparently less developed in the direction of a lush bryophyte dominated vegetation than other communities on branch segments of similar thickness (TABLE 3).

DISCUSSION

Like any ecological community, the epiphyte community in the canopy is not static but changes in terms of its component species and their abundance. The structure of the community at a given moment is determined by (1) the suitability of the habitat for certain species and by (2) characteristics of the preceding invading species.

Habitat properties are taken here to include a vast range of ecological factors including the disturbance regime. Characteristics of the habitat will affect within-community processes such as the species displacement rate which in turn will depend on the species involved. Just as the canopy communities are dynamic, so are their habitats, due to (among other reasons) species induced changes (e.g. microclimate) and the expansion of the tree crown.

In addition to the quality and quantity of the invading species, the arrival sequence may also influence the structure of bryophyte and lichen communities (Schuster 1957; Barkman 1958). The importance of priority effects was shown experimentally for aquatic microcosms (Robinson & Dickerson 1987).

The relative importance of propagule supply and habitat properties as determinants of community structure is not easily assessed. A role for propagule supply is acceptable in particular for the younger, partially still unoccupied, substrates. However, the observed trends in the diversity pattern in this study suggest that within-community processes are also of importance, especially in later successional stages. First, there is no apparent correlation between sample area and richness, $r_s = -0.006$; $p = 0.94$ (FIGURE 5). Second, species richness decreases significantly with the age of the substrate, $r_s = -0.75$; $p = <0.0001$, even though the time available for the arrival of new species is, presumably, longer (FIGURE 1). Third, the predominance of species increases in time (FIGURE 4), paralleled with an increase in biomass, thickness of the bryophytic layer and thickness of the amount of accumulated epiphytic organic soil (TABLE 2). With the expansion of the tree crown, changing habitat conditions favor the development of large-patch forming bryophytes, replacing a species rich, fine grained, middle canopy vegetation.

Interestingly, dominance of species appears associated with late successional stages. The log-series model (Fisher *et al.* 1943) has been described for such a dominance-diversity relation-

TABLE 2. Structural characteristics of four canopy community types in the Upper Montane Rain Forest at Santa Rosa de Cabal. The community types A through D represent a gradient from outer towards inner canopy.

Community type	A Outer canopy	B →	C →	D Inner canopy
No. of samples	25	32	47	47
Average branch diameter (cm)	1.8	12.6	15.9	25.4
Number of liverwort taxa	46	55	23	51
Number of moss taxa	6	18	63	16
Number of macro lichen taxa	38	35	31	20
Number of bryophyte and macro lichen taxa	90	108	111	97
Average cover of lichens (%)	48.7	35.6	9.2	3.5
Average cover of bryophytes (%)	16.6	52.9	83.3	94.3
Average biomass (g/dm ²)	1.6	5.4	6.7	8.2
Average thickness of the bryophyte layer (cm)	1.2	2.7	5.5	9
Average thickness of the suspended soil layer (cm)	<0.1	0.2	1.4	9

ship and is usually believed to best fit pioneer communities (Whittaker 1975). In contrast, Hughes (1986) predicted in his dynamics model that few species would attain dominance in stable environments as a result of competition. In concordance with the dynamics model, the dominance-diversity curves are hollow due to relatively many rare species (FIGURE 6). The log-series model predicts 'less hollow' curves (Hughes 1986).

The epiphytic habitat is usually not regarded as stable (e.g. Benzing 1990). Stable conditions in the canopy of this particular Upper Montane Rain Forest are evidenced, however, by the high amounts of epiphytic biomass that may attain an estimated 44 tons ha⁻¹, a quantity that exceeds by threefold that reported from other sites at lower altitudes (Hofstede et al. 1993). Accumulated suspended soil is the major component of this mass, building a layer on branches of up

to 60 cm thickness (Wolf 1993b). Stability of the epiphyte vegetation in this cool and wet Upper Montane Rain Forest may be high due to low animal activity, low wind velocities, and high longevity of the host trees. As to the latter, a woodcore, at breast height, of an average sized *Weinmannia mariquitae* canopy tree yielded a ¹⁴C date of 215 ± 15 years (Hofstede et al. 1993). Moreover, the development of the bryophyte dominated epiphytic vegetation in the cool and wet montane rain forest should be relatively rapid (Proctor 1990).

Even though not universally true, highest species richness occurs at a moderate standing crop, roughly between 2 and 7 g/dm² (FIGURE 3). Diversity is often a unimodal function of productivity, both in animal and in plant communities (e.g. Rosenzweig & Abramsky 1993). Epiphyte vegetation may lend itself particularly well to evaluate this pattern since the difficult esti-

TABLE 3. Community characteristics of two community groups occupying branches or trunks of diameter ≥ 10 cm. Group 1, indicated as open circles in FIGURE 4, consists of a group of samples that do not adhere well to the trend of increasing dominance with diameter. Values are sample averages.

	Group 1 (N = 7)	Group 2 (N = 52)
Thickness of the suspended soil layer (cm)	0.5	3.0
Thickness of the bryophyte layer (cm)	4.3	7.1
Biomass (g/dm ²)	3.9	6.7
Cover of lichens (%)	23	9.0
Cover of bryophytes (%)	58	85
Number of taxa	22	14
Number of taxa/dm ²	2.45	2.0

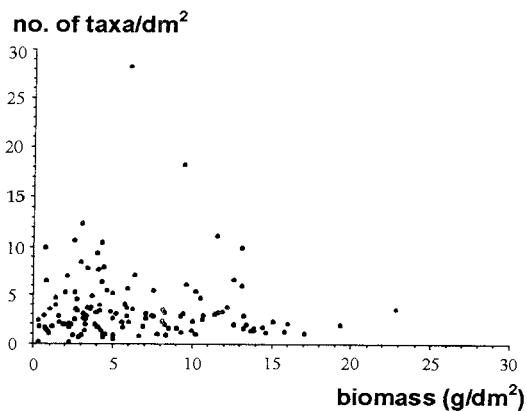


FIGURE 3. Biomass (g dryweight/dm²) and non-vascular epiphyte species richness (S/dm²).

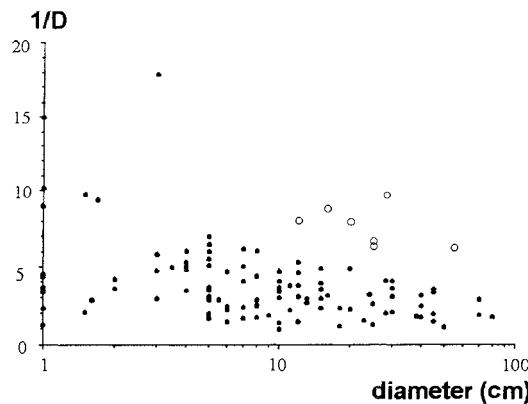


FIGURE 4. Branch or trunk diameter (cm) and Simpson's diversity ($1/D$), an index which emphasizes the relative abundance of species. Low diversity is thus equivalent to low evenness or high dominance. The open circles indicate a group of seven samples that do not adhere to the trend of increasing dominance with diameter.

mation of underground biomass is avoided. When we accept an inverse correlation between productivity and disturbance, intermediate disturbance may be the key factor.

In the many hypotheses that have been put forward to explain the correlation between diversity and productivity or disturbance, usually competition is regarded as an important process, in particular for the decrease phase (Rosenzweig & Abramsky 1993). The two authors rightfully noted that if species at an undisturbed or highly productive site are removed from a patch through competition, this should result in a depauperate assemblage of the same community. The stand-

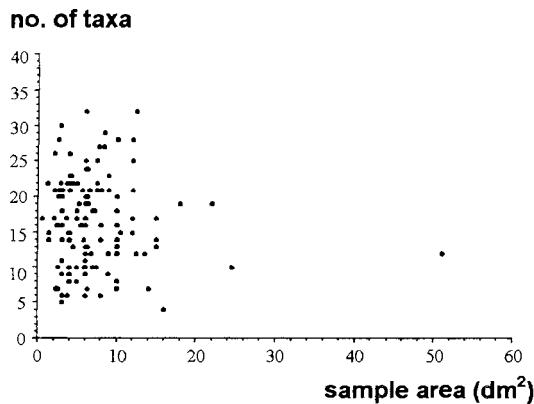


FIGURE 5. Sample size (dm^2) and non-vascular epiphyte species richness (S).

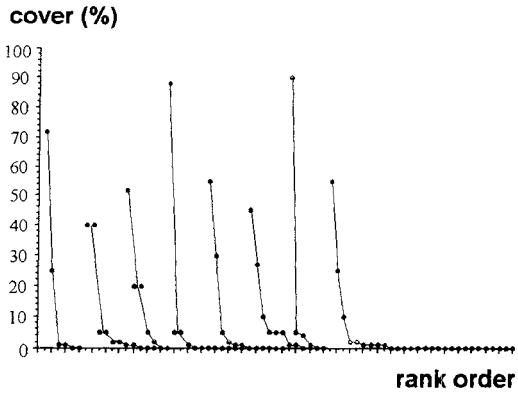


FIGURE 6. Dominance-diversity curves for those canopy communities that attained the highest biomass, i.e. $> 14 \text{ g dryweight}/\text{dm}^2$. Abundance is estimated as percentage cover.

ing crop-diversity relationship is normally demonstrated among vegetation types (e.g. Grime 1973; Al-Mufti et al. 1977). Within the same vegetation type, a relationship between standing crop and species richness could not be demonstrated in wetlands (Moore & Keddy 1989). In this study, the four community types have many species in common, forming a single community type of higher rank, and each type has few exclusives (TABLE 1). In other words, the potential for many species to occur in the species-poor highly productive sites on the thicker branches is apparently there, supporting the idea that competitive exclusion is important.

Competition is likely to take place mainly for available space, since non-vascular epiphytes

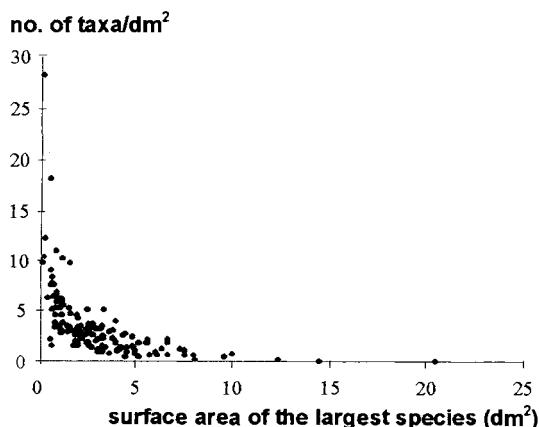


FIGURE 7. Surface area (dm^2) of the species occupying the largest area within the community and non-vascular epiphyte species richness (S/dm^2) of that community.

TABLE 4. Trends in succession of epiphyte communities in the canopy.

Successional stage	Position in the canopy	Community structure					
		Biomass	Cover	Richness	Evenness	Main components	Characteristic growth forms
Early	outer canopy	moderate	ca. 70%	high	high-moderate	fruticose lichens	closely appressed lichens and pendent cryptogams
Middle	middle canopy	moderate	ca. 100%	moderate	moderate-low	bryophytes and foliose lichens	loosely attached lichens and turf or mat building bryophytes
Late	inner canopy	high	ca. 100%	low	low	liverworts	tall turfs

form single-layered communities and are often thought to be dependent on atmospheric inputs for the bulk of their nutrient and water requirements (Brown & Bates 1990). In a possible reaction, many lichens and in particular bryophytes exhibit vigorous horizontal growth.

In conclusion, I propose that competition for available space largely determines the structure of late successional epiphyte communities. Further support for this hypothesis comes from the good inverse correlation, $r_s = -0.8$; $p < 0.0001$, between the surface area of the largest species (usually one individual plant) and species richness of the community (FIGURE 7).

The successional stage nearest to climax is not characterized by a single dominant species. In fact, similarity between stands of the *Plagiochila fuscolutea* community is less than within any other community type (Wolf 1993b). At different sites any species out of a group of 'climax' species, e.g. *Bazzania hookeri*, *Chorisodontium mittenii*, *Lepicolea pruinosa*, *Plagiochila fuscolutea*, and *Porotrichodendron superbum*, may prevail (TABLE 1). Minor habitat differences or priority effects offer an explanation.

Summarizing the observed patterns, three successional stages may be recognized that correspond with the changing relative position of the community within the expanding tree crown (TABLE 4). Structural changes of the community with age apparently reflect a shifting balance from the importance of the supply of propagules towards competition. The youngest branches are colonized out of the species pool of the outer canopy *Diplasiolejeunea pauckertii*-*Usnea* spp. (A) community; this pool is comparable in size with that of other community types. The species richness per unit twig surface area, however, is relatively high. In the outer canopy, competitive interactions are less likely to influence the variety since biomass and cover values are relatively low. In accordance with predictions by the dynamics model, evenness is high (Hughes 1986). On

branches of intermediate thickness, the variety is less, and thick inner canopy branches finally support a high biomass bryophyte community particularly poor in species. Here, dominance is high and competition presumably most severe.

The pattern in succession presented here is merely a trend (TABLE 3). Local disturbances, extreme habitat conditions, such as sun exposure, rain tracks, steeply inclined branches, herbivory and unknown factors, may interrupt or impede succession. In addition, the sequence of the invading species may affect successional seres. The arrival time of large-patch forming bryophytes may be crucial. In the present study, the static method of data-gathering applied does not allow discernment between habitat differences and propagule supply as determinants of community structure. Long-term monitoring of epiphyte vegetation in the canopy is recommended.

ACKNOWLEDGEMENTS

The assistance with identification of many specialists is gratefully acknowledged, in particular that of Dr. S. R. Gradstein (liverworts), Drs. G. B. A. van Reenen (mosses) and Dr. H. J. M. Sipman (lichens). I thank Dr. M. González-Espinoza for his valuable comments on the manuscript. The study was supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO, grant W84-236).

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